

Particulate Versus Integrated Evolution of the Upper Body in Late Pleistocene Humans: A Test of Two Models

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KEY WORDS Hominid paleontology, Neandertals, Early modern humans

ABSTRACT Evolutionary biologists are largely polarized in their approaches to integrating microevolutionary and macroevolutionary processes. Neo-Darwinians typically seek to identify population-level selective and genetic processes that culminate in macroevolutionary events. Epigeneticists and structuralists, on the other hand, emphasize developmental constraints on the action of natural selection, and highlight the role of epigenetic shifts in producing evolutionary change in morphology. Accordingly, the ways in which these paradigms view and address morphological contrasts between classes of related organisms differ. These paradigms, although seldom explicitly stated, emerge in paleoanthropology as well. Considerations of postcranial morphological contrasts between archaic and modern humans typically fall into one of two broad interpretive models. The first derives from the neo-Darwinian perspective and holds that evolution in the postcranial skeleton was largely mosaic (operating in a *particulate* manner), and that temporal change in specific traits informs us about behavioral shifts or genetic evolution affecting isolated anatomical regions (i.e., adaptive behavioral inferences can be made from comparative studies of individual trait complexes). The alternative model follows from the epigeneticist paradigm and sees change in specific postcranial traits as correlated responses to change in overall body form (involving shifts in regulation of skeletal growth, or selective and developmental responses to broad adaptive shifts). By this view, *integration* of functional systems both constrains and directs evolution of various traits, and morphological contrasts inform us about overall change in body form related to change in such things as overall growth patterns, climatic adaptation, and technological dependency. These models were tested by confirmatory factor analysis using measures of upper body form and upper limb morphological traits in Eurasian Neandertal and early modern fossils and recent human samples. Results indicate (1) a model of morphological integration fits the data better than a model of no integration, but (2) this integration accounts for less than half of the variance in upper limb traits, suggesting a high degree of tolerance for particulate evolution in the context of an integrated upper body plan. Significant relationships were detected between joint shapes and body size, between humeral shaft shape and body size and chest shape, and between measures of biomechanical efficiency and robusticity. The

Received November 8, 1994; accepted March 17, 1996.

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observed morphological differences between late archaic and early modern humans reflect particulate evolution in the context of constraints imposed by genetic and morphological integration. While particulate approaches to interpreting the fossil record appear to be justified, attention must also be paid to delineating the nature and extent of morphological integration and its role in both constraining and producing observed patterns of variation between groups. Confirmatory factor analysis provides a means of examining trait covariance matrices, and serves as a useful method of identifying patterns of integration in morphology. © 1996 Wiley-Liss, Inc.

Paleoanthropology, while having its own historical development and conceptual concerns, is subject to many of the same paradigmatic issues that pervade the fields of study with which it articulates. As would be expected, conceptual frameworks (and conflicts) from evolutionary biology find expression in debate concerning processes and patterns in human evolution. One argument revolves around explanatory models of evolutionary change in form. At issue is the degree to which macroevolutionary events (and attendant phenotypic shifts) can be explained as extrapolations of microevolutionary processes (an essentially neo-Darwinian perspective: Fisher, 1930; Mayr, 1963; Williams, 1966; Lewontin, 1974; Charlesworth et al., 1982) vs. emergent, epigenetic developmental shifts understandable only by reference to processes operating at higher levels of organization (Waddington, 1957; Gould, 1980; Alberch, 1980; Oster and Alberch, 1982). Related to this issue is the question of the strength of integration of the phenotype.

Some morphologists have sought overarching laws of form (Russell, 1916), most often citing developmental patterns and epigenetic events as the primary causal mechanisms regulating morphological transitions between phenotypes (e.g., Thompson, 1917; Gould, 1980; Oster and Alberch, 1982). This thinking finds its greatest expression in the structuralist paradigm of developmental and evolutionary biologists such as Goodwin, Webster, and Hall (Webster and Goodwin, 1982; Goodwin and Trainor, 1983; Hall, 1983; Goodwin, 1984). The epigenetic integration of developmental processes limits the possible forms of the resulting phenotype, thus producing constraints on the

amount of phenotypic variation available to selection. Support for this position is found in the "homologous series" of Vavilov (1922; Gould, 1984; see also Oster and Alberch, 1982) and in the phenomenon of phenocopies (Goldschmidt, 1940). By this view, we might expect a predominant pattern in the fossil record of morphological stasis interrupted by correlated morphological shifts in multiple traits associated with shifts in the organismal *bauplan*, or pattern of trait integration (see Gould and Lewontin, 1979; Smith et al., 1985; Levinton et al., 1986; Sterns, 1986; Raff et al., 1987).

A related concept is that the identification of allometric relationships between body size and morphological variation constitutes a complete explanation of phenotypic change. Pilbeam and Gould (1974), for example, concluded that the craniofacial contrasts between gracile and robust species of *Australopithecus* reflect geometric similarity and functional equivalence of masticatory systems in light of temporal increases in body size. In short, that the australopithecines are all "... scaled variants of the 'same' animal" (Pilbeam and Gould, 1974:900; see also Wolpoff, 1973, 1974). This interpretation contrasts with more adaptationist explanations positing a dietary shift in the genus through time (e.g., Kay, 1975, 1985). Another example lies in Vrba's (1994) hypothesis that hominid evolutionary brain size expansion is attributable to hyperpedomorphosis related to late Cenozoic cooling trends, rather than selection for intelligence per se.

Others seek more particularistic, and usually adaptationist, explanations in keeping with the neo-Darwinian emphasis on the role of microevolutionary processes in explaining larger scale patterns of morphologi-

cal evolution. This approach generally entails "atomization" of organisms into individual characters whose evolution can be explained in terms of allelic variation, selection, and drift operating at the population level (Fisher, 1930; Lewontin, 1974; Charlesworth et al., 1982). Neo-Darwinians point to the abundant heritable variation of most simple metrical traits and to the occurrence of rapid change in mean phenotype of such traits under artificial selection (Lewontin, 1974; Falconer, 1981; Charlesworth et al., 1982; Wagner, 1984) as justification for atomization of the organism. This is arguably the normative paradigm in comparative studies of hominid anatomy. This has led to an emphasis on studies of functional (biomechanical) rather than body size allometry (see Smith, 1993), and to an unfortunate reliance on post hoc interpretations of genus and species level morphological contrasts (Fleagle, 1979; Gould and Lewontin, 1979; Smith, 1982).

The role of developmental constraints on morphological evolution is central to debate about macroevolutionary processes (see, e.g., Alberch, 1980, 1982; Gould, 1980; Charlesworth et al., 1982; Lande, 1986). These two points of view are not necessarily incompatible, but attempts to reconcile them have been few (but see Cheverud, 1984; Wake and Larson, 1987). Even from a strict neo-Darwinian perspective, it is legitimate to ask if selection is more frequently operating on canalization of morphogenesis (which is itself under genetic control: Waddington, 1957) or on individual traits.

Parallels to these paradigms in evolutionary biology can be found in explanative models of human morphological evolution. Neo-Darwinian and epigeneticist arguments are implicit in research on the anatomical differences separating premodern and modern humans. Morphological contrasts between Eurasian archaic and anatomically modern humans (both fossil and recent) can be observed in virtually every aspect of the skeleton. In the postcranial skeleton, these contrasts include aspects of bone size, robusticity, and details of morphology (see reviews in Trinkaus, 1983a; Hambucken, 1993), as well as more general features of body form, including body size (Fraye, 1984;

Feldesman et al., 1990), trunk shape (Franciscus, 1989; Ruff, 1991; Churchill, 1994a,b), and limb proportions (Trinkaus, 1981; Stringer, 1984; Holliday and Trinkaus, 1991).

By far the most prevalent interpretive framework uses traits, both in isolation and in combination, to infer adaptive and/or phylogenetic meaning from evolutionary change or stasis in morphology. Basic to this neo-Darwinian approach is the assumption that traits selected for study are functionally or phylogenetically relevant. Support for this approach comes from the observation that morphological evolution in the later Pleistocene was mosaic (i.e., skeletal traits varied in their degrees and rates of change: Trinkaus and Smith, 1985; Trinkaus et al., 1991). While confounding genetic effects cannot be ruled out (e.g., pleiotropy, linkage disequilibrium, and change in regulator genes affecting heterochrony), mosaic patterns of change suggest that different traits were differently influenced by genetic evolution (especially that driven by selection) and developmental plasticity. Given the well documented plasticity of cortical bone in responding to its biomechanical environment (references in Ruff, 1992; Trinkaus et al., 1991, 1994; Ruff et al., 1993), analysis of some traits has the potential to inform about hominid behavior at a fine-grained level. At the heart of this broad, *particularist* approach to interpreting the fossil record is the idea that specific morphological contrasts are meaningful in and of themselves, and that their analysis provides a framework for understanding late Pleistocene human adaptive evolution and a basis for evaluating competing phylogenetic models of the origins of modern humans.

The alternative (epigeneticist) view is that many of the morphological contrasts between late archaic and modern humans are simply correlates of differences in overall body form between these two groups (i.e., epiphenomena of global morphogenetic processes). The need for integration of parts in the musculoskeletal system may require that as some aspects of the system change (such as size) concerted changes must occur throughout the system to maintain functional congruence. Thus morphological differences in cranial and postcranial form be-

tween groups may merely reflect differences in body size, overall skeletal robusticity, thoracic shape, and limb proportions, which in turn were responding to larger-scale factors, such as changes in climate, diet, and culture (especially overall technological dependency). In this *integrationist* view specific morphological contrasts may be telling us less about detailed aspects of hominid behavior or populational affinities and more about broader-scale patterns of hominid adaptation and evolution.

It can be argued that paleontological approaches to archaic/modern human morphological contrasts cannot be so simply dichotomized, and that all analyses incorporate some aspects of both paradigms. Still, this polarization of approaches is a useful heuristic device that makes explicit different ideas about how evolution in the human body proceeded. Without question, there is integration in all biological systems (due to genetic and developmental integration: Cheverud, 1984; Smith et al., 1985; Stearns, 1986; Zelditch, 1987, 1988), and especially in biomechanical systems, necessary to maintain functional equivalence in light of changes in organismal size and shape (Bookstein et al., 1985; Corruccini, 1987; Smith, 1993). *The question here is to what degree this integration (in conjunction with evolution in body form) accounts for postcranial morphological contrasts between hominid groups.* Was the shift from archaic to modern morphology primarily the result of shifts in the organization and regulation of developmental patterns (i.e., a change in bauplan) or the accumulation of more independent changes in single characters over time?

This issue has important implications for our understanding of evolution in the genus *Homo*. If postcranial traits that differentiate Neandertals and modern humans such as scapular axillary border morphology (Stewart, 1962; Trinkaus, 1977) or pubic ramis length (Stewart, 1960; Trinkaus, 1976) are correlates of gracilization or trunk shape changes (which may themselves be intercorrelated), then the modern human morphotype may have arisen independently on different occasions in the context of selection operating on overall body form. If this is the case, then the worldwide appearance of "mo-

derenity" in geographically separate populations might be expected with a shift in grade from archaic to modern behavior (favoring a more gracile body type) or with general evolutionary trends for gracility (Smith, 1985). A shared bauplan in members of the genus *Homo* makes reversion to developmental default states under relaxed selection not only possible, but likely (Wake, 1991). Thus the essentially independent origin of modern human morphology in different regions of the Old World (as indicated by the multiregional evolution model of modern human origins) can be explained by technological evolution and diffusion without reference to orthogenesis (Wolpoff et al., 1984; Smith, 1985). Also, the appearance of modern morphology in the Skhul and Qafzeh hominids (McCown and Keith, 1939; Vandermeersch, 1981) may represent a degree of parallelism *unrelated to the phylogenetic origins of anatomically modern humans*. Particularist approaches, on the other hand, generally see morphological change as reflecting adaptive evolution; hence the contrasts between Levantine late archaic and early modern humans are thought to reflect adaptive behavioral differences between them (Trinkaus, 1992b, 1993; see also Lieberman and Shea, 1994). Adherents to the integrationist approach just as easily see larger-scale body form changes as arising from either broad-scale adaptive (since climatic or cultural selection on body form can change genetic and phenotypic correlations between characters: see Charlesworth et al., 1982) or nonadaptive, stochastic events effecting regulation of ontogeny, thus calling into question interpretations of adaptive differences between these groups (Tillier, 1989). Thus the adaptive significance of archaic/modern human morphological contrasts remains at issue.

UPPER BODY CONTRASTS BETWEEN LATE ARCHAIC AND EARLY MODERN HUMANS

A number of morphological contrasts exist between archaic (in this study represented by Eurasian Neandertals) and modern humans [including both recent (Holocene) peoples and early modern humans from the late

Pleistocene]¹. Table 1 provides a summary of some of the main differences in the upper body between these groups. Contrasts in specific upper limb traits are numerous (many of which involve differences in relative frequencies of traits rather than presence/absence: see Trinkaus, 1983a; Ham-bucken, 1993, 1994), and only those traits that most frequently enter into adaptive, phylogenetic/taxonomic, or integrative arguments are considered in this study. A thorough review of particularist uses of upper limb traits is detailed in Churchill (1994a) and summarized in Table 1.

Integrationist arguments have predominately taken two forms. The first of these holds that the principal body form shift in the Pleistocene involved robusticity and muscularity, and that many of the specific morphological contrasts in the craniofacial and postcranial skeleton (including long bone lengths and diaphyseal shapes, joint shapes and orientations, and muscle marking morphologies) are correlates of gracilization. Gracilization came about through technological development (hence less need for somatic effort: Brace 1962, 1991; Montagu, 1968; Brose and Wolpoff, 1971; Smith, 1985), or through an endocrine shift affecting development of the musculoskeletal system (Keith, 1925; Brothwell, 1975; Riesenfeld, 1975; Weaver, 1980; Kennedy, 1985, 1992; Hublin, 1992), or both. The second integrationist model holds that change in chest shape altered the positions of bones in the pectoral girdle, changed muscle lines of action and biomechanical stress trajectories, and thus influenced postcranial morphology (see McCown and Keith, 1939; Smith, 1976;

Churchill and Trinkaus, 1990). These arguments are provided in more detail elsewhere (Churchill, 1994a).

If evolutionary change was truly mosaic, then various traits can be independently considered in functional and phyletic analyses (although arguments about the relevance of these traits must still be supported). If intercorrelation is an important part of understanding within- and between-group variability in traits, then it may make more sense to focus on evolutionary change in overall body form ("baseline" traits like robusticity) and its causes. Phylogenetic questions can then be phrased in terms of these baselines (i.e., can body form change be explained by continued adaptation to local environmental conditions and evolving material culture, or can it be explained only by elevated gene flow or population replacement from other regions?). The phylogenetic and taxonomic relevance of isolated postcranial traits can be readily assessed by examining their correlations with these baselines (traits little influenced by the baselines can more confidently be used as phyletic markers because they are less prone to homoplasies related to adaptive change in body form). Attempts to explicitly examine the effect of body form parameters on long bone and joint shape (e.g., Trinkaus et al., 1991) are few. More clearly defining the role of these factors is important because it is currently unclear whether or not the morphological dichotomy between late archaic and modern humans reflects an adaptively significant behavioral dichotomy (see Tillier, 1989; Wolpoff et al., 1991; vs. Trinkaus, 1992a).

MATERIALS AND METHODS

The question of whether or not postcranial evolution in the later Pleistocene was *truly* mosaic (i.e., there was a high degree of tolerance for particulate change on top of an integrated genus *Homo* upper body plan) can be addressed through analysis of correlations between traits. Strong integration of elements would be expected to manifest itself as a strong pattern of covariance between morphological variables (Olson and Miller, 1958) in both fossil and recent humans. If overall change in body form accounts for

¹Based on current fossil evidence, most aspects of Neandertal upper limb morphology are either plesiomorphous for members of the genus *Homo* or synapomorphous with modern humans (Trinkaus, 1989). Thus Neandertals are used here to represent late archaic humans generally. In addition, upper body morphology is variable within and between modern human populations, and Neandertal morphology may be similar to that of *some* modern groups in *some* traits (e.g., Neandertals may share with Eskimos shorter distal limb segments, larger thoraces, and heightened robusticity, but differ from Eskimos in other traits). Nonetheless, no modern populations are known to combine all the characteristics of the Neandertal upper body, and the concept of a general Neandertal/modern human dichotomy is basically valid.

TABLE 1. Commonly cited upper body postcranial contrasts between late archaic and early/recent modern humans

Trait	Archaic characteristics	Applications ¹	References
<u>General body form</u>			
Stature	Short stature ²	—	Fruyer, 1984; Feldesman et al., 1990; Trinkaus, 1983b
Laterality	M-L wide trunks; broad, muscular shoulders	Adaptive arguments	Trinkaus, 1983b; Ruff et al., 1993
Chest shape	A-P deep chests	Adaptive arguments	Fanciscus, 1989; Churchill, 1994a,b
Postcranial robusticity	Heightened muscularity and joint/diaphyseal robusticity	Taxonomic trait ^{3,4} and character state in phylogenetic arguments	Day and Stringer, 1982; Smith et al., 1983; Kennedy, 1984a,b; Stringer et al., 1984; Stringer, 1987, 1993; Stringer and Andrews, 1988; Wolpoff, 1989
		Adaptive arguments	Trinkaus, 1987, 1989, 1992; Ben-Itzhak et al., 1988; Trinkaus and Ruff, 1989a,b; Ruff et al., 1993
Limb proportions	Low limb-to-trunk length ratios, short distal limb segments	Adaptive arguments	Trinkaus, 1981
		Phylogenetic arguments	Stringer, 1984; Holliday and Trinkaus, 1991; Holliday et al., 1993
<u>Upper limb morphology⁵</u>			
Scapular axillary border	High frequency of dorsal sulci	Taxonomic trait	Smith, 1984
		Phylogenetic arguments	Jelínek, 1989; Smith and Trinkaus, 1991; Fruyer, 1992a,b; Wolpoff, 1992; Fruyer et al., 1993
Scapular glenoid shape	Long and narrow	Adaptive arguments	Trinkaus, 1977
		Phylogenetic arguments	Smith and Trinkaus, 1991
Humeral torsion	Low torsion angle	Adaptive arguments	Churchill and Trinkaus, 1990
		Taxonomic trait	Boule, 1911–1913
Humeral deltoid tuberosity shape	Narrow deltoid tuberosity	Adaptive arguments	Vandermeersch and Trinkaus, 1995
		Taxonomic trait/phylogenetic arguments	Endo, 1971; Thoma, 1975; Smith et al., 1989
Humeral diaphyseal shape	Midshaft platybrachia	Taxonomic trait/phylogenetic arguments	Thoma, 1975; Smith et al., 1983; Trinkaus, 1983b
		Adaptive arguments	Ben-Itzhak et al., 1988
	Medullary stenosis	Taxonomic trait/phylogenetic arguments ⁴	Kennedy, 1983, 1984a,b, 1985, 1992
		Adaptive arguments	Churchill, 1993, 1994a; Ruff et al., 1994
Proximal ulnar morphology	Anteriorly oriented trochlear notch	Taxonomic trait	Thoma, 1975; Rightmire and Deacon, 1991; Churchill et al., in press
		Adaptive arguments	Trinkaus, 1989, 1992b
Radial tuberosity position	Medially oriented tuberosity	Adaptive arguments	Trinkaus and Churchill, 1988
Biomechanical efficiency	High power arm/load arm ratios in arm and forearm	Adaptive arguments	Trinkaus, 1983a, 1984

¹“Adaptive arguments” include broad-scale adaptive differences (e.g., morphological adaptation to cold) as well as claims of behavioral contrasts between archaic and early modern humans; “taxonomic arguments” include assertions that a trait is characteristic of a hominid group as well as attempts to assign a particular fossil to a given group; “phylogenetic arguments” include attempts to evaluate the transitional aspects of various fossils and broader arguments about the origins of modern humans.

²Stature is of course highly variable in modern populations, but Neandertals’ mean stature is on the low end of the modern human range of means and is below that of Eurasian early modern humans.

³Either postcranial robusticity used as defining trait of premodern humans or postcranial gracility used as a defining trait of anatomically modern humans.

⁴General long bone robusticity or medullary stenosis (not confined to the humerus).

⁵Excluding the wrist and hand.

most of the seemingly mosaic change in postcranial features, then measures of body form across fossil and recent samples should covary with specific postcranial features. Confirmatory factor analysis (CFA: Mulaik, 1975; Dillon and Goldstein, 1984; Jöreskog and Sörbom, 1989) provides a means of testing a priori ideas about how body form "factors" condition variation in specific morphological variables. Wake and Larson (1987:47) argue that both neo-Darwinian and epigeneticist methods are required to attain a complete explanation of morphological transitions: "The epigenetic rules of development underlying these transformations are identified from structuralist analysis, whereas the fixation of different structures and their combination to construct novelties are investigated as Darwinian evolutionary processes." Confirmatory factor analysis serves as one means of identifying latent "epigenetic rules" of development by isolating morphological intercorrelations that may relate to developmental (or functional) constraints on organismal design (see also Cheverud, 1984). At issue is the strength of constraints on selection in the evolution of the genus *Homo*. Is human postcranial skeletal variation uniformly distributed in multivariate space (like Galton's polyhedron, as discussed by Gould, 1980), as we might expect if all traits are free to vary, and their variation between groups reflects the unique genetic evolutionary and adaptive histories of various populations? Or is morphological variation organized around a limited number of vectors through multidimensional space, as we might envision if the effects of selection were constrained by overriding developmental epigenetic interactions or a limited number of "workable" functional morphological designs? Analysis of trait covariance structure gives us a method of gaining insight into the nature of constraint and particulate modes of evolution (Cheverud, 1984). This paper uses CFA to address morphological contrasts in the upper limb and shoulder, and asks: is late Pleistocene evolution in the upper limb largely the result of body form changes (predominately integrationist), or of differential selection and plasticity operating across individual features of the limb (predominately particularist)?

Samples and measurements

Modern human populations vary in general body form, with mean values overlapping the range of variation seen in Neanderthals in stature (Feldesman et al., 1990), chest depth and width (Churchill, 1994a,b), and skeletal robusticity (Ruff et al., 1993; Churchill, 1993). Assuming a similar pattern of trait covariance between archaic and anatomically modern humans (i.e., that the pattern of integration was the same between groups), if the integrationist model holds then body form factors should account for a large amount of the variance in specific upper limb traits across both archaic and modern human populations. Data on Eurasian late archaic and early anatomically modern human samples were combined with data from recent human samples to test the integrationist and particularist models.

In composing a recent human comparative data base the goal was to sample as wide a range of variation in size, robusticity, and thoracic shape as possible. Only "prime-aged" adults (i.e., long bone epiphyses fused but not of advanced age based on dental wear, ectocranial suture closure, pubic symphyseal morphology, and presence and degree of vertebral osteophytosis) were included in the samples.

Data were collected on four recent human populations: autopsy samples of European and African Americans, and archeological samples of Pueblo AmerIndians and Aleutian Islanders. The EuroAmerican sample (25 males, 20 females: Maxwell Museum of Anthropology and Smithsonian Institution) represents an industrialized population (hence relatively low activity level and relatively gracile) with a temperate or cold-temperate body form and limb proportions reflecting European ancestry (Roberts, 1978; Holliday and Trinkaus, 1991). EuroAmericans, with AfroAmericans, also represent the upper portion of the range for stature in the comparative groups (Eveleth and Tanner, 1976). The AfroAmerican sample (25 males, 25 females: Smithsonian Institution) represents a population of comparable behavioral and economic background to the EuroAmericans but with a body form and limb proportions more representative of

tropical ancestry² (Todd and Lindala, 1928; Roberts, 1978; Tanner et al., 1982; Feldesman et al., 1990).

A sample of late Puebloan (Pueblo III/IV) AmerIndians (20 males, 20 females: Maxwell Museum) from the central Rio Grande Valley of New Mexico represent sedentized yet active agriculturalists (of moderate robusticity: see Ruff and Hayes, 1983; and Ruff et al., 1984; Bridges, 1989, on AmerIndian agriculturalists in general). AmerIndians retain some elements of an arctic-adapted body form, such as relatively deep chests and short distal limb segments (Newman, 1953, 1960; Hulse, 1960; Roberts, 1978). Pueblo AmerIndians represent the middle-to-lower end of the range of human stature among these samples (Hrdlička, 1930). Western Aleuts (25 males, 22 females: Smithsonian Institution) represent a high activity (and high robusticity: Laughlin et al., 1991; Laughlin, 1993; Berget and Churchill, 1994) population. In body form the Aleuts are similar to arctic adapted Eskimos, having relatively short distal limb segments and large, anteroposteriorly deep chests (Hrdlička, 1945; Laughlin, 1949, 1951). Aleuts also represent the lower end of the size range for stature in these samples (Laughlin, 1949, 1951). Gender was determined in the archaeological samples from pelvic and cranial remains.

The Neandertal sample ($n = 19$ individuals, plus isolated elements from the sites of Krapina and Vindija; Table 2) includes specimens from western and central Europe and the Near East. Early modern humans ($n = 65$) are represented by the Mousterian-associated hominids from Skhul and Qafzeh and by fossils associated with European Upper Paleolithic assemblages (Table 2).

To examine body form and upper limb morphological integration, variables were chosen to represent body form parameters and specific morphological features of the upper limb (Table 3). Three aspects of body form were considered: body size, chest shape, and

TABLE 2. *Fossil specimens*

<u>Neandertals</u>	
Amud 1	
La Chapelle-aux-Saints 1	
La Ferrassie 1, 2	
Kebara 2	
Krapina (42 isolated elements)	
Lezetxiki 1	
Neandertal 1	
La Quina 5	
Régourdou 1	
Shanidar 3	
Shanidar 1, 4, 5, 6, 8	(Data from Trinkaus, 1983b, and from casts)
Spy 1, 2	
St. Césaire 1	
Tabun 1	
Vindija (4 isolated elements)	
<u>Early modern humans</u>	
Abri Pataud 4, 5	
Arene Candide 2, 4, 5, 10, 12, 13, 14, 15	
Baoussou da Torre 2	
Barma Grande 2, 3, 5	
Bruniquel 24	
Cap Blanc 1	
Chancelade 1	
Cro-Magnon 1, 2, 3	
Dolni Vestonice 13, 14, 16	
Farincourt 1	
Gough's Cave 1	
Grotte des Enfants 4, 5	
La Madeleine 1	
Mladeč 23, 24, 25a,c	
Neuëssing 2	
Obercassel 1, 2	
Paglicci 25	
Paviland 1	
Le Placard 16	
Předmostí 3, 4, 9, 10, 14	(Data from Matiegka, 1938)
Qafzeh 3, 7, 8, 9	
Rochereil 1	
La Rochette 1	
Romanelli 1, 4	
Romito 3, 4	
Skhul II, IV, V, VI, VII	
Stetten 3	
St. Germain-la-Rivière 4	
Veyrier 1, 5-1, 7, 9, 10	

robusticity. Overall body size was represented by the geometric mean (GEOMEAN) of humeral articular length, radial articular length, and clavicular maximum length (operational definitions for all of the variables are provided in the Appendix). This measure thus combines aspects of both linear body size ("stature" as represented by humeral and radial lengths) and laterality (as represented by clavicular length).

Upper chest shape was represented by two variables, second rib chord (R2C) and biiliac breadth (BIB). R2C is taken as a measure of the anteroposterior depth of the upper rib cage. The second rib was chosen for a number

²African Americans are in fact intermediate in relative limb proportions between African and EuroAmerican populations (Ruff and Walker, 1993), but are more similar to tropical populations than any of the other recent human samples.

TABLE 3. Variables used in the confirmatory factor analysis

Variable ¹	Standardization	Measure of . . .
GEOMEAN	None	general size
R2C	Residual R2C on GEOMEAN	chest AP depth
BIB	Residual BIB on GEOMEAN	chest ML width
35%J	Residual $^4\sqrt{35\%J}$ on HAL	diaphyseal robusticity (distal)
HDAA	Residual $^2\sqrt{HDAA}$ on HAL	articular robusticity
RTA	Residual $^2\sqrt{RTA}$ on HAL	muscularity
50%MA	Residual $^2\sqrt{50\%MA}$ on HAL	medullary area (midshaft)
GLENOID	Residual GAB on GAL	joint shape
TROCH	Residual OHT on CHT	joint shape
TORSION	None	diaphyseal shape
50% θ	None	diaphyseal shape (midshaft)
DELTOID	Residual DTP on HAL	biomechanical efficiency
BICEPS	Residual HNL on RAL	biomechanical efficiency

¹Operational definitions of variables are provided in the Appendix.

of reasons: (1) The scapula occupies the space between the external surfaces of the second and seventh ribs, thus upper rib cage shape should have the greatest effect on scapular orientation and upper limb morphology. (2) Ribs in fossil specimens, and to a lesser extent recent human archeological skeletons, tend to be highly fragmentary. The second rib tends to be better represented in these cases than the longer ribs from lower in the series. (3) The second rib is readily identifiable, reducing the error inherent in trying to sequence fragmentary ribs from incomplete rib cages. (4) R2C spans the distance from the vertebral articulation to the sternal cartilage, and thus should be a reasonably good measure of the anteroposterior depth of the upper thorax (based on the degree of concordance between mean chest AP diameter taken on extant populations and mean R2C taken on skeletal samples representative of those populations, $r = 0.83$; Churchill, 1994a). Even given the generally better preservation of the second rib relative to other ribs, it was still necessary to predict R2C for 25 fossil specimens (three Neanderthals and 22 early modern humans). This was accomplished using multiple regression based on the medial length of the clavicle (from the sternal end to the conoid tubercle) and humeral deltoid tuberosity circumference (rationale for the choice of variables and details of the regression are provided in Churchill, 1994a). BIB is a measure of lower, not upper, trunk breadth (Ruff, 1991) and is only moderately correlated with upper chest breadth in the living (r between mean chest ML diameter in the living populations and

mean BIB in representative skeletal samples = 0.31; Churchill, 1994a). Given the usually poor preservation of fossil rib remains (and the inability to reasonably predict the subtense of the second rib from other upper body measures), BIB was used as the best available measure of upper chest breadth.

Postcranial robusticity cannot be considered as a single trait (Churchill, 1994a), thus radial tuberosity area (RTA) was used as a measure of upper limb muscularity, humeral distal articular area (HDAA) as a measure of joint size, and cross-sectional polar moment of area of the mid-distal humerus (35%J) as a measure of diaphyseal strength. Given that the relative size of the medullary cavity enters into integrationist arguments about gracilization³, medullary area of the midshaft humerus (50%MA) was included as an inverse measure of robusticity⁴.

To reduce the effect of size on the chest shape and robusticity measures, each variable was regressed on an appropriate size-standardizing variable and the residuals were used in the analysis. R2C and BIB were

³Elevated steroid-mediated endosteal bone apposition has been proposed to account for the observed pattern of "medullary stenosis" seen in premodern human long bones (see Kennedy, 1985; but see Ruff et al., 1994).

⁴The magnitude of the polar moment of area is a function of both the amount and distribution of cortical bone in the section. Accordingly, there generally exists a correlation between medullary area and polar moment of area at any given level along a diaphysis. Thus J was determined at 35% and MA at 50% of HAL to reduce somewhat the effect of intercorrelation of these variables.

regressed on GEOMEAN⁵. For robusticity measures, the appropriate nth-root was taken for measurements expressed in units of higher order (i.e., square root of areal measurements, fourth root of second moments of area), and then each measure was regressed on humeral length.

Variables were selected to measure joint- and muscle-marking morphology, humeral shaft shape, and biomechanical efficiency. These measures, the “dependent variables,” reflect traits that are often used in phylogenetic and functional analyses of archaic/modern human contrasts (Table 1). These variables reflect the “shape” of morphological traits, and have been most often examined in the past by constructing ratios between two variables. To avoid problems inherent in using ratios in multivariate techniques (distributional problems and incomplete partialing out of size: Albrecht et al., 1993), each variable was regressed on the appropriate size-standardizing variable and the resulting residuals were used in the CFA. Angular measurements were left untransformed.

The form of the scapular axillary border (the most widely used postcranial trait in arguments about the origins of modern humans; Table 1) and radial tuberosity orientation could only be defined as categorical variables, and hence were not appropriate for factor analysis. Accordingly, the relationship of these aspects of muscle-marking morphology to body form are considered elsewhere (Churchill, 1994a). The relative width of the deltoid tuberosity (DELTWID) was thus used as the only measure of muscle-marking morphology. Joint shapes and orientations were represented by two variables: scapular glenoid fossa shape (GLENOID) and the orientation of the ulnar trochlear notch (TROCH). Humeral shaft shape was repre-

sented by humeral torsion angle (TORSION) and by midshaft cross-sectional theta (50% Θ). Theta measures the angle between the plane of greatest bending rigidity and the midcoronal axis of a cross section. Finally, relative biomechanical efficiency was represented by the power arm/load arm relationships of *M. deltoideus* (DELTOID) and *M. biceps brachii* (BICEPS).

The question of limb proportion differences between Neandertals and modern humans was not specifically addressed in this analysis. It may be that some aspects of “biomechanical efficiency” reflect changes in limb proportions (load arms becoming longer in modern humans without a concomitant change in power arms). If this is the case, we would expect to find these reflections of biomechanical efficiency to be at least somewhat correlated with thoracic shape across groups, since both limb proportions and thoracic shape are expected to respond to cold adaptation following Bergmann’s and Allen’s rules (Bergmann, 1847; Allen, 1877).

Unless otherwise noted in Table 2, all measurements were taken on the original fossils and comparative skeletons by me. For comparative modern human samples, either the right or left upper limb was selected at random for analysis. For fossil specimens, the more complete upper limb was used, with values for the opposite side being substituted for missing values when possible.

Data analysis and confirmatory factor analysis (CFA) models

All of the residuals and angles were tested for univariate normality using D’Agostino’s Omnibus K^2 statistic (D’Agostino, 1990) in NCSS 5.03 (Hintze, 1991) as a substitute for testing for multivariate normality (see Dillon and Goldstein, 1984). Residuals of two variables—BIB and Deltwid—were found to be non-normally distributed. Log transformation of DELTWID and recalculation of the residuals from regressions in log-log space did not improve the shape of the distribution. This variable was thus dropped from the analysis (see Results). For BIB, the distribution of residuals suffered from skewness as the result of two outliers on the left side of the curve. These two specimens were assigned BIB values two and one units, respec-

⁵R2C was predicted for 25 fossils from medial clavicular length and humeral deltoid tuberosity circumference. While neither of these measures enters directly into GEOMEAN, the geometric mean does incorporate clavicular maximum length, which is naturally highly correlated with clavicular medial length. Using the residual of predicted R2C on GEOMEAN could, then, produce smaller residuals than would be expected from the same regression using actual R2C. This treatment is, however, limited to 25 of 266 individuals in the analysis, and recalculation of the CFA using the recent humans only did not appreciably alter the outcome.

tively, below the value of the next smallest individual. This method solves the problem of skewness while preserving the deviancy of the cases (Tabachnick and Fidell, 1983). Normality of the univariate distribution of BIB could not be rejected after this treatment of the outliers.

Confirmatory factor analysis was used to test the fit of the particularist and integrationist models to the data. When the analysis is conducted on dispersion matrices, the chi-square goodness-of-fit statistic is the likelihood ratio for the hypothesis that covariation in the data is constrained according to the model (Zelditch, 1987). Provided that the models are hierarchical, analysis of the covariance structure allows for both statistical evaluation of the fit of the models to the data, plus direct comparison of the amount of explanatory information contained in each model (Bentler and Bonett, 1980).

Pairwise treatment of missing values was used in the construction of the variance-covariance matrix. This method is valuable for fossil samples in which most individuals are missing values for one or more variables, but can result in matrices with negative eigenvalues (and consequent inflation of positive eigenvalues) which can distort statistics derived from the matrix (Norušis, 1990). The 13 eigenvalues from this covariance matrix were all positive, which supports the use of pairwise estimation in this case.

It is possible that sets of traits may be highly intercorrelated (with one another and with body form parameters) within groups, but that groups differ in patterns of covariance of traits. Thus combining all the fossil and recent groups in a single analysis would tend to lower covariance estimates and might cause rejection of the integrationist model even though variation in body form was causing most variation in upper limb traits. A test for equality of covariance matrices between groups (Box, 1949) was used to evaluate the level of similarity in the organization of upper body integration. First, dispersion matrices for all the modern human groups were tested for homogeneity, both as a single test with five matrices and as 10 separate pairwise tests between two groups. None of the tests rejected the null hypothesis that the dispersion matrices were equal

across samples. Thus the modern human samples were pooled and a new dispersion matrix was derived for the combined sample. The dispersion matrix for the Neandertal sample was then tested against the pooled modern human matrix, and again homogeneity of the matrices could not be rejected.

The integrationist and particularist models provide a basis for constructing, a priori, hypothetical models which specify how the body form and upper limb morphological variables relate to common latent factors, and how these factors relate to one another. Three nested or hierarchical models were constructed, from simple (M_0 : no integration) to more complex (M_1 : body form factors account for most of the variability in upper limb traits; M_2 : body form factors *plus* specific upper limb factors account for the variation).

The fit of the models was evaluated using the linear structural relationship package (LISREL 7: Jöreskog and Sörbom, 1989) in SPSS (Norušis, 1990). LISREL allows for specification of several parameters of the model to be tested. The basic factor model is:

$$X = \Lambda f + e$$

where X = a p -dimensional vector of observed variables, f = a q -dimensional vector of unobservable (latent) common factors, e = a p -dimensional vector of unobservable unique factors, and Λ = a $p \times q$ matrix of unknown constants called factor loadings. The p unique factors are assumed to be uncorrelated with each other, thus $ee' = \Psi$, a diagonal matrix of unique factor loadings. The variance-covariance matrix Σ_{xx} can thus be decomposed:

$$\Sigma_{xx} = \Lambda \Phi \Lambda' + \Psi$$

where $\Phi = aq \times q$ matrix of correlations between the common factors. The hypothetical models to be tested allow for a priori specification of how the variables should relate to the common factors (i.e., we can specify the individual factor loadings in the matrix Λ) and how the common factors should relate to one another (i.e., we can specify the form of matrix Φ).

If there is no *overriding* integration in operation, as predicted by the particularist

paradigm, the upper limb morphological variables should be largely uncorrelated with the baseline factors, i.e., they are unconstrained and can adapt via selection and developmental plasticity to their group-specific functional environments. Factor analysis would thus be expected to do a poor job of explaining variance in these traits. A model of "no integration" was constructed that restricted the loading of the morphological traits on the body form factors. This model served as the "null model" (M_0) (Bentler and Bonett, 1980) against which improvements in fit of the more complex models could be evaluated.

Under the integrationist paradigm, evolution in the upper limb is correlated with evolution in general aspects of body form (because integration of functional systems both necessitates concerted change across the system as body form evolves *and* constrains the independent evolution or plasticity of specific skeletal traits). We would then expect the expression of morphological traits like joint shapes and sizes, long bone diaphyseal morphology, muscle-marking shapes and orientations, and bone-muscle lever systems to covary significantly with baseline morphological parameters due to the need to maintain an integrated, functioning system in light of variation in overall form. In factor analytical terms, one would expect the three general factors to account for most of the variance in these traits. Thus a model was constructed in which the morphological variables were relatively unconstrained in their loadings on the three body form factors. The basic integrationist model (M_1) tested is given as a path diagram in Figure 1.

There may exist a correlation between general body size and chest shape, but the variables used to represent chest shape in the model are residuals from regressions of chest dimensions on GEOMEAN, the size variable. Thus the correlation between these two factors should equal zero. A correlation may also exist between the size and robusticity factors. Robusticity in the strict sense is the amount of structural material in an element relative to some measure of body size (Ruff et al., 1993). All of the robusticity variables used here are residuals of raw variates regressed on humeral length. Humeral

length is a measure of linear body size (stature), but does not necessarily reflect other variables contributing to the mass of the upper limb (e.g., muscularity or differences in the distribution of body mass between groups). Some residual correlation may remain between these factors, thus the correlation was left unrestricted in this model. There may also exist a correlation between thoracic shape and robusticity, both because more active individuals may require greater vital capacity and hence larger chests, and because of sample composition (the most robust groups—Neandertals and Aleuts—are also those tending to have large chests). The correlation between these two factors was also left unrestricted in this model. The factor correlation matrix was thus fixed as:

$$\Phi = \begin{bmatrix} 1 & & \\ 0 & 1 & \\ \phi_{13} & \phi_{23} & 1 \end{bmatrix}.$$

The matrix of factor loadings, Λ , was also predetermined for the basic integrationist model. The joint shape variables were left free to load on any of the factors. Allometric relationships between joint shape and body size are not uncommon (e.g., Falsetti et al., 1993), and it is also possible that some joint shapes change with change in overall robusticity (see Trainkaus et al., 1991). Change in thoracic shape, by changing the position of the scapula, may also affect upper limb joint configurations. Humeral shaft shape likely correlates with both chest shape and robusticity related to positioning of the humerus relative to the shoulder girdle and activity effects during the individual's lifetime. There is, however, no *a priori* reason to expect measures of humeral diaphyseal shape to be correlated with body size, so the loading of these variables on the size factor was restricted (set to zero). There is also no *a priori* reason to expect measures of biomechanical efficiency to be related to body size under this model. A clear relationship with robusticity should exist if selection or developmental plasticity operates to maximize both the strength and leverage of skeletal elements in highly active populations. Chest shape may also correlate with measures of upper limb biomechanical

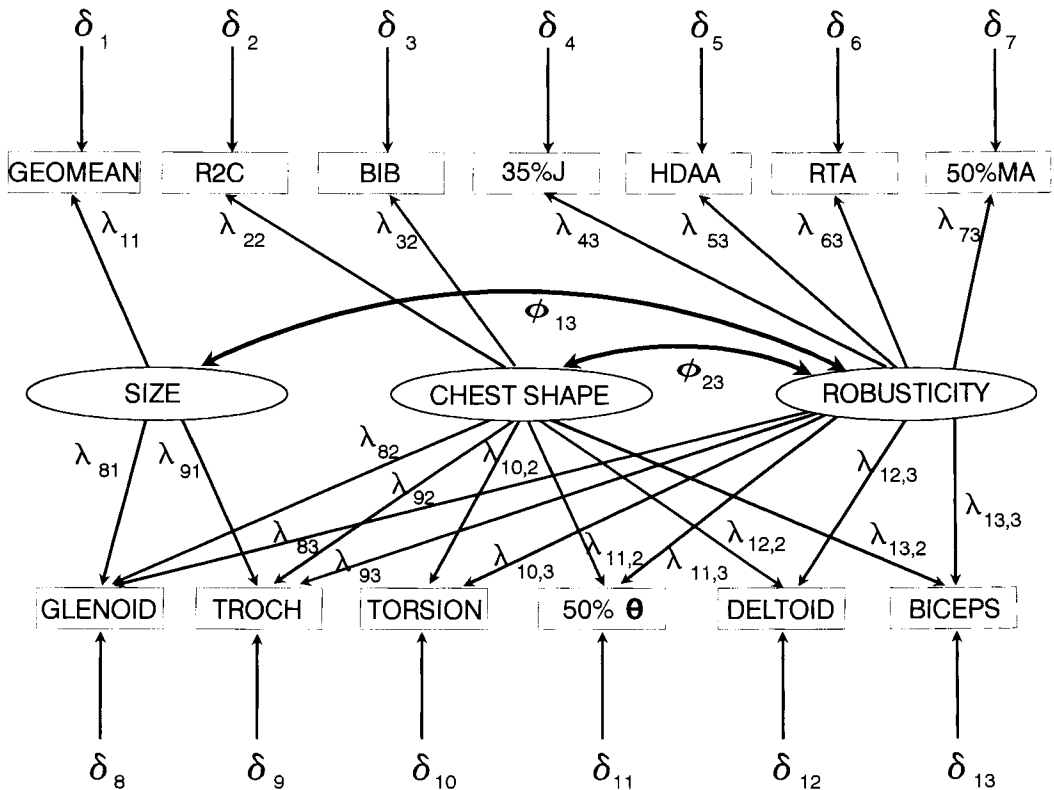


Fig. 1. Path diagram representing the basic body form integration model. The three common factors hypothesized to account for the correlations between observed variables are body size, chest shape, and robusticity. The "independent" variables used to represent these factors are placed across the top, the "dependent" variables that are of ultimate concern in the analysis are represented on the bottom row. δ = unique variance associated with each variate.

efficiency via cold adaptation (between-group differences in power/load arm relationships may reflect limb segment shortening without a concomitant decrease in muscle power arms). Since selection sufficient to produce shortened distal limb segments would also be expected to affect trunk shape (following Bergmann's and Allen's rules), these measures might be expected to correlate with the chest shape factor.

Overall body size may play a role in the expression of all of the "dependent" variables in this analysis, and following a true integrationist argument, all of the dependent variables should be left free to load on all of the factors. LISREL provides output tables of modification indices that specify the improvement in fit if restricted variable-factor

loadings were freed. Thus I chose to start with a more restricted model and to explore the improvements in the fit of the model gained by freeing some of the variable's loadings on certain factors. The Λ matrix entered into the analysis is proved in Table 4.

Even if strong integration is in action, it is possible that body form factors alone cannot account for the covariance between upper limb traits. It may well be that additional latent factors, reflecting integration of bio-mechanical systems *within* the upper limb, must be specified to more fully define the nature of human upper body integration. Thus an expanded integrationist model, in which the Λ matrix was extended to include three additional factors, was tested. This number of factors was chosen because the

TABLE 4. Hypothetical factor pattern derived from the basic integrationist model (M_1) (see Fig. 1)¹

	Body size	Chest shape	Robusticity
GEOMEAN	λ_{11}	0	0
R2C	0	λ_{22}	0
BIB	0	λ_{32}	0
35%J	0	0	λ_{43}
HDAA	0	0	λ_{53}
RTA	0	0	λ_{63}
50%MA	0	0	λ_{73}
GLENOID	λ_{81}	λ_{82}	λ_{83}
TROCH	λ_{91}	λ_{92}	λ_{93}
TORSION	0	$\lambda_{10,2}$	$\lambda_{10,3}$
50% Θ	0	$\lambda_{11,2}$	$\lambda_{11,3}$
DELTOID	0	$\lambda_{12,2}$	$\lambda_{12,3}$
BICEPS	0	$\lambda_{13,2}$	$\lambda_{13,3}$

¹ Fixed parameters are indicated by 0, nonzero factor coefficients estimated by LISREL are indicated by λ . Operational definitions of variables are provided in the Appendix.

“dependent” variables fall into three groups (joint shape, humeral diaphyseal shape, and biomechanical efficiency), and we might expect that the analysis will minimally detect common factors uniting variables within these groups. The basic integrationist model was left unchanged, and three factors, each relating to two of the dependent variables, were added (Fig. 2, Table 5). Since there were also no a priori arguments for how the factors should relate to one another under this model, the factor correlation matrix, Φ , was entered as a standard matrix (all diagonals set at one, all off diagonals free to vary).

RESULTS

Correlations between the variables used in the CFA were generally low (Table 6). Examination of the significant coefficients shows the highest r-values between the measures of robusticity and muscularity. There is also a cluster of significant r-values between R2C and some of the robusticity variables, which is not surprising given that the most robust groups in the sample (Aleuts, Neandertals) also have the deepest chests. The two measures of humeral diaphyseal shape, TORSION and 50% Θ , both show significant but low (negative and positive, respectively) correlations with the chest shape variables. TORSION is also negatively correlated with skeletal robusticity variables, which may reflect the intercorrelation of ro-

busticity and chest shape. There is also a cluster of significant correlations between the measures of biomechanical efficiency and some of the measures of robusticity and muscularity. Again, most of these r-values are low, indicating at best a moderate degree of integration between the chosen variables.

To further examine the possibility that between-group (archaic vs. modern) differences in the pattern of integration were affecting the observed correlations, the matrix was also constructed using only the recent human (all fossils excluded) groups. With only slight exceptions, the pattern, signs, and relative magnitudes of the significant correlation coefficients did not change with this change in sample composition (Table 7).

The adequacy of the data to factor analysis was evaluated using the Kaiser-Meyer-Olkin test (in SPSS: Kaiser, 1974). This test produced a relatively low value for the sampling adequacy statistic ($KMO = 0.65622$). In addition, the multiple R^2 s between each variable and every other variable (communalities) were also generally low (Table 8), and principal components factor extraction resulted in only 64.5% of the total variance being accounted for by the first six factors.

These results suggest that there do exist covariance relationships between variables that can be explained by reference to latent factors, but these factors will be able to account for only a portion of the total variance. Thus there is indeed integration in operation, but there is also a significant degree of tolerance for particulate variance within the general upper body plan. The remaining task is to determine to what extent integrative models enhance our understanding of upper body evolution in the later Pleistocene.

The results of the CFA are presented in Table 9. None of the models produced a significant fit with the data. Since the chi-square variate is a direct function of sample size, rejection of even adequate models is to be expected with large n (Bentler and Bonnett, 1980). Thus a means of evaluating the difference in fit of the models, and hence the increase in information gained with increasingly complex models, is required. The incremental fit index (Bentler and Bonnett, 1980) was used for this purpose. For comparing

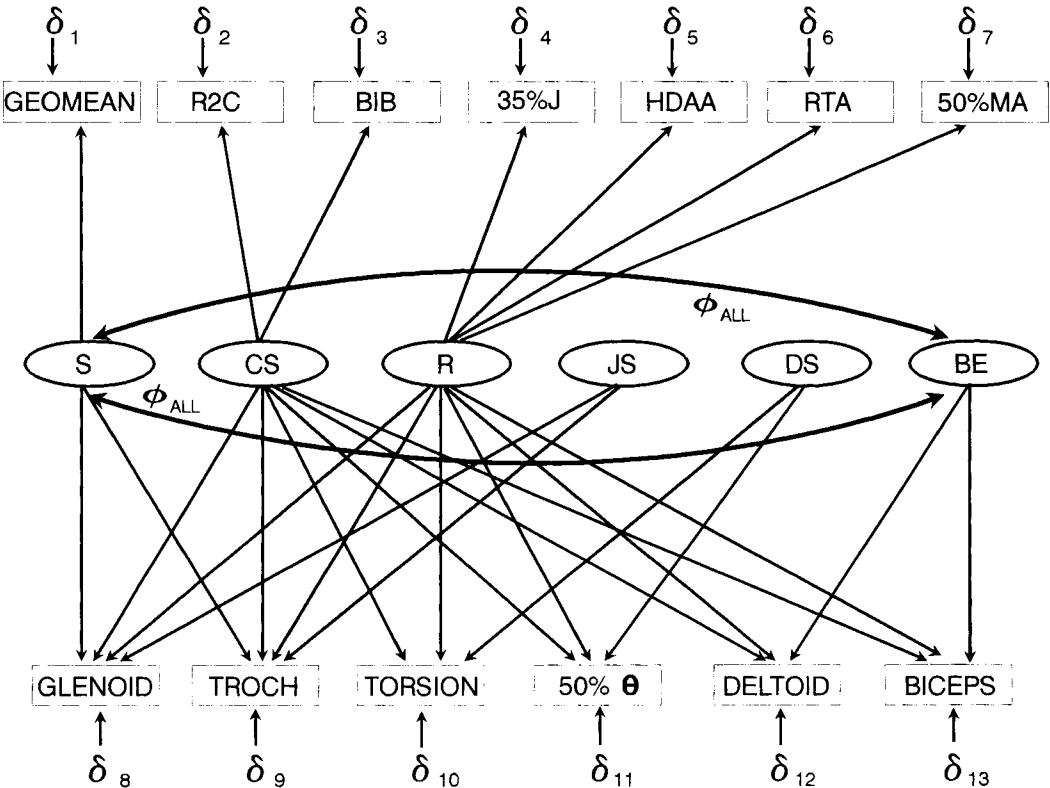


Fig. 2. Path diagram representing the expanded (body form + upper limb) integration model. Three additional factors, reflecting integration unique to the upper limb, have been added: a joint shape factor (JS), a diaphyseal shape factor (DS), and a biomechanical efficiency factor (BE). Only one intercorrelation between factors is drawn (Φ_{ALL}) to represent the possibility of every possible correlation under this model. Individual lambdas are omitted for the sake of clarity.

TABLE 5. Hypothetical factor pattern reflecting latent body form and upper limb factors (expanded integrationist model, M_2) (Fig. 2)

	S ¹	CS	R	JS	DS	BE
GEOMEAN	λ_{11}^2	0	0	0	0	0
R2C	0	λ_{22}	0	0	0	0
BIB	0	λ_{32}	0	0	0	0
35%J	0	0	λ_{43}	0	0	0
HDAA	0	0	λ_{53}	0	0	0
RTA	0	0	λ_{63}	0	0	0
50%MA	0	0	λ_{73}	0	0	0
GLENOID	λ_{81}	λ_{82}	λ_{83}	λ_{84}	0	0
TROCH	λ_{91}	λ_{92}	λ_{93}	λ_{94}	0	0
TORSION	0	$\lambda_{10,2}$	$\lambda_{10,3}$	0	$\lambda_{10,5}$	0
50% θ	0	$\lambda_{11,2}$	$\lambda_{11,3}$	0	$\lambda_{11,5}$	0
DELTOID	0	$\lambda_{12,2}$	$\lambda_{12,3}$	0	0	$\lambda_{12,6}$
BICEPS	0	$\lambda_{13,2}$	$\lambda_{13,3}$	0	0	$\lambda_{13,6}$

¹S = size, CS = chest shape, R = robusticity, JS = joint shape, DS = diaphyseal shape, BE = biomechanical efficiency.
²Fixed parameters are indicated by 0, nonzero factor coefficients estimated by LISREL are indicated by λ . Operational definitions of variables are provided in the Appendix.

nested models M_0 , M_k , and M_t , the fit index is calculated as:

$$FI = (Q_k - Q_t)/(Q_0 - 1),$$

where for a given model $Q = (v/df)$.

Fit indices (Table 9) show the three-factor integrationist model to improve almost 50% over the model of no integration ($FI_{M_0-M_1} = 0.4809$), while the six-factor integrationist model improves by only about 22% over the model of no integration ($FI_{M_0-M_1} = 0.2167$). While the incorporation of body form factors contributes to the explanatory power of the model, the added complexity of the three additional upper limb factors does not significantly improve the model, and in fact reduces the overall fit of the model.

TABLE 6. Correlation matrix of variables used in confirmatory factor analysis

	GEOMEAN	R2C	BIB	35%J	HDAA	RTA	50%MA	GLENOID
R2C	-0.0000	—						
BIB	-0.0018	0.3817	—					
35%J	0.1420	0.2232	0.0629	—				
HDAA	0.1360	0.2116	-0.0445	0.6717	—			
RTA	0.0709	0.0922	-0.0553	0.5427	0.4331	—		
50%MA	0.0210	0.2763	0.2065	0.3369	0.2562	0.1894	—	
GLENOID	0.1159	-0.0996	-0.1060	-0.0190	0.0564	-0.0775	0.1557	—
TROCH	0.2910*	-0.1111	-0.0209	0.0563	0.0778	0.0768	-0.0428	0.1025
TORSION	0.0871	- 0.2927	- 0.2695	- 0.2176	- 0.2082	-0.1078	-0.0888	0.0774
50%Θ	- 0.3073	0.2282	0.2614	0.1235	-0.0502	-0.0922	0.1875	-0.0632
DELTOID	-0.0168	0.0952	0.0633	0.1755	0.1604	0.2358	0.1684	-0.0560
BICEPS	0.1128	0.1339	0.0264	0.2036	0.2788	0.2897	0.0812	-0.1437
TROCH	TORSION	50%Θ	DELTOID					
TORSION	-0.0374	—						
50%Θ	-0.1047	-0.0465	—					
DELTOID	0.0071	-0.0668	0.0786	—				
BICEPS	0.0496	-0.0562	-0.1412	0.1186				

* Bold indicates values significant at $P \leq 0.01$. Operational definitions of variables are provided in the Appendix.

TABLE 7. Correlation matrix of variables used in confirmatory factor analysis—recent humans only

	GEOMEAN	R2C	BIB	35%J	HDAA	RTA	50%MA	GLENOID
R2C	-0.0068	—						
BIB	-0.0194	0.3887	—					
35%J	0.1448	0.2273	0.0487	—				
HDAA	0.1327	0.2092	-0.0446	0.6774	—			
RTA	0.0492	0.0805	-0.0553	0.5892	0.4478	—		
50%MA	0.0411	0.2936	0.2289	0.3710	0.2846	0.2807	—	
GLENOID	0.1242	-0.1012	-0.0821	0.0253	0.0823	-0.0426	0.1038	—
TROCH	0.2805*	-0.1127	-0.0471	0.0218	0.0775	0.0232	0.0582	0.2305
TORSION	0.1002	- 0.2935	- 0.2486	- 0.2335	- 0.2171	-0.0542	-0.1432	0.0332
50%Θ	- 0.2877	0.2448	0.3026	0.1220	-0.0518	-0.0239	0.1000	-0.1299
DELTOID	-0.0365	0.0885	0.0547	0.2002	0.1640	0.2021	0.1957	-0.0436
BICEPS	0.0990	0.1306	0.0016	0.1984	0.2950	0.2490	0.1481	-0.1072
TROCH	TORSION	50%Θ	DELTOID					
TORSION	-0.0006	—						
50%Θ	-0.0269	-0.1050	—					
DELTOID	0.0177	-0.0459	0.1302	—				
BICEPS	-0.0147	0.0118	-0.0911	0.1032				

* Bold indicates values significant at $P \leq 0.01$. Operational definitions of variables are provided in the Appendix.

TABLE 8. Communalities of variables¹ used in the confirmatory factor analysis

GEOMEAN	0.62706
R2C	0.56983
BIB	0.66963
35%J	0.71987
HDAA	0.66327
RTA	0.62360
50%MA	0.56089
GLENOID	0.67868
TROCH	0.44922
TORSION	0.38893
50%Θ	0.54984
DELTOID	0.20074
BICEPS	0.45246

¹ See the Appendix for definitions of variables.

Modification indices produced by LISREL indicate that, for the three-factor model, freeing 50%Θ on the size factor (F_1) would decrease the chi-square statistic by approximately 11.4, and freeing 50%MA on the chest shape factor (F_2) would further improve the fit of the model (χ^2 would decrease by approximately 7.1). Freeing both of these restricted loadings, however, would reduce the chi-square statistic by only approximately 18.5 and would decrease the degrees of freedom by 2. Even with these loadings freed, the model still does not adequately fit the data ($\chi^2_{df53} = 82.19, P = 0.006$).

When factor analysis is conducted on the

TABLE 9. Comparison of models of no integration (M_0), body form integration (M_1), and body form + upper limb integration (M_2)

Model	Factors ¹	Chi-square	df		FI ²
No integration	0	179.50	69	$P < 0.001$	
Body form	3	100.69	55	$P < 0.001$	0.4809
Body form + upper limb	6	114.96	51	$P < 0.001$	-0.2167

¹ Number of common factors to explain upper limb trait covariance.² Fit index relative to model of no integration.TABLE 10. Confirmatory factor analysis solution for the integrationist model¹

	Size	CS	Robust.	Θ_e
GEOMEAN	0.597	0.0 *	0.0 *	0.644
R2C	0.0 *	0.715	0.0 *	0.489
BIB	0.0 *	0.549	0.0 *	0.698
35%J	0.0 *	0.0 *	0.877	0.235
HDAA	0.0 *	0.0 *	0.764	0.420
RTA	0.0 *	0.0 *	0.611	0.630
50%MA	0.0 *	0.293	0.372	0.863
GLENOID	0.182	-0.151	-0.015	0.942
TROCH	0.490	-0.076	-0.041	0.759
TORSION	0.0 *	-0.366	-0.137	0.818
50% Θ	-0.396	0.364	-0.061	0.877
DELTOID	0.0 *	0.081	0.208	0.941
BICEPS	0.0 *	0.025	0.292	0.910
Factor correlation matrix:				
1.0 *				
0.0 *	1.0 *			
0.302	0.304	1.0 *		
Goodness of fit statistic:				
$\chi^2 = 86.73$, 53 df				
$P = 0.002$				

¹ Asterisks indicate fixed parameters, bold indicates loadings significant at $P \leq 0.01$, Θ_e = the unique variance for each observed variable. See the Appendix for definitions of variables.

correlation matrix, the factor loadings represent simple correlations between the latent factors and observed variables (Child, 1970). Since information about the covariance structure is contained in the three-factor body form model (M_1), and it would be useful to know which of the variables are most strongly influenced by body form changes, this model was retested on the correlation matrix (with 50% Θ freed on the size factor and 50%MA freed on the chest shape factor as indicated by the first analysis). The factor solution is given in Table 10.

A few observations can be made about the factor loading patterns [these observations also follow from examination of the (weak) correlations between variables in the original correlation matrix (Table 6)].

The improvement of fit of the basic integrationist model (M_1) over the null model

(M_0) is a function of (1) a seeming size effect on joint shapes and 50% Θ , (2) a relationship between chest shape and humeral diaphyseal shape (including 50%MA), and (3) a relationship between robusticity and biomechanical efficiency variables. All of these significant loadings are moderate to weak.

Joint shapes appear to be responding somewhat to variation in overall size. TROCH produces a significant loading on the size factor. The loading of GLENOID on the size factor is not significantly different from zero, but the correlation coefficient is close to reaching significance (significance tests of factor loadings were conducted using an $n = 174$, the average n for all of the pairwise r -values in the original correlation matrix). Humeral shaft shape is also clearly linked to variation in overall size and chest shape. The negative loading of TORSION on the chest shape factor indicates that larger-chested (in both AP and ML dimensions: Table 6) individuals tend to have more dorsally directed humeral heads. The insignificant loading of TORSION on the robusticity factor suggests that the chest shape-TORSION relationship is more a function of scapular position on the thorax (with larger-chested individuals having more sagittally oriented scapulae) than of a covariance of both of these things with activity.

The two measures of biomechanical efficiency have weak but significant loadings on the robusticity factor, again suggesting that robusticity and power/load arm relationships are linked. The moderate correlation between the size and robusticity factors shows that the size standardization of the robusticity variables did not entirely remove the effects of overall size on these variates. This may be the result of sexual dimorphism in size and robusticity (males tend to be both

larger and more robust than females), or it may reflect inadequacy of regression-adjusted residuals for size standardization (Corruccini, 1987).

The moderate correlation between the robusticity and thoracic shape factors indicates a weak but clear relationship between these aspects of body form. Still, it is not possible to discern with this data the nature of the causal factors underlying this relationship. It should again be stressed, however, that the weak relationships detected between these factors and variables make these results merely suggestive, and it is clear that variation in body form parameters accounts for relatively little of the variance in upper limb features. The poor fit of the basic integrationist model is also reflected in the high values of the estimates of unique variance (Θ_e) of the dependent variables, many of which approach unity (Table 10). Although this solution is detecting some weak relationships between the dependent variables and the hypothesized factors, the poor fit of the model indicates that correlated change in body form parameters is not sufficient to explain most of the variance in the upper limb traits under study.

DELTWID was dropped from this analysis due to its skewed distribution in the pooled sample. This problem with the distribution was a function of inclusion of Neandertals, with very narrow deltoid tuberosities, into the pooled sample. When Neandertals are removed from the sample, normality of the distribution could not be rejected. Partial correlation analysis was then conducted, examining each body form measure with DELTWID while holding all other body form measures constant. No significant relationships were detected between DELTWID and any of the body form measures.

DISCUSSION

Although the basic integrationist model was rejected in the CFA (as were all the models), it did produce an improvement in fit over the model of no integration. The patterns of the weak correlations between upper limb traits and body form factors indicate that there is a degree of integration that must be considered in morphological studies

of the upper limb. Since some aspects of robusticity are more developmentally plastic than others, the intercorrelation of three types of robusticity measures suggests that selection history and plastic remodeling have parallel effects on bone strength. In third-class lever systems (as with *M. deltoideus* and *M. biceps brachii*) in which the epiphyseal growth plate is positioned between the muscle attachment site and the axis of rotation of the joint, biomechanically stimulated growth at the metaphysis (Arkin and Katz, 1956; Tardieu and Trinkaus, 1994) would serve to proportionally lengthen the muscle power arm. Thus the loadings of the measures of mechanical efficiency on the robusticity factor may reflect a developmental response to high activity, a genetically mediated adaptation for greater upper limb strength, or both. Additional work on this subject is needed to more fully understand the effects of bony remodeling on adult morphology.

The relationship detected between aspects of humeral diaphyseal shape and chest shape lends credence to the idea that chest shape differences between hominid groups may contribute to upper limb morphological differences (McCown and Keith, 1939; Smith, 1976; Churchill and Trinkaus, 1990). However, a direct influence of rib cage shape on some muscle-marking measures in the upperlimb is not evident in this data. The partial correlation analysis of DELTWID and chest shape failed to detect a relationship. Elsewhere (Churchill, 1994a) I examined the relationship of axillary border morphology to chest shape variables using analysis of variance (with the axillary border types used as class variables and chest shape measures as the response variables). Neither chest AP depth (R2C) nor width (BIB) were significantly different between axillary border types.

The finding of a moderate degree of trait interdependence, combined with apparent homogeneity of the covariance matrices across groups, suggests that there is a single *Homo sapiens* upper body pattern of trait integration or "bauplan" that did not change substantially with the appearance of modern humans. Within this bauplan there appears to be a considerable amount of tolerance for

particulate modes of morphological change, through selection, developmental plasticity, and stochastic genetic changes. Differential sensitivity and response to biomechanical stimuli by different aspects of the skeletal system (Ruff et al., 1991; Ruff and Runestad, 1992; Trinkaus et al., 1994) likely play a large role in reducing overall covariance between traits and producing seemingly mosaic patterns of morphological differences between hominid groups. The finding of homogeneity of covariance matrices across groups suggests, however, that either the amount of particulate morphological change was insufficient to alter covariance patterns, or that genetic and functional integration of morphology acted to constrain the degree of particulate change. The observed morphological differences between late archaic and early modern humans reflect particulate evolution in the context of constraints imposed by genetic and morphological integration.

Integrative models emphasizing skeletal gracilization in late Pleistocene evolution are not supported by this analysis. If a shift in endocrine-mediated bone growth was responsible for late archaic/modern human contrasts in skeletal robusticity and other features, we would minimally expect to find an inverse relationship between long bone medullary cavity size and other measures of robusticity (see Kennedy, 1985). Instead, the factor analysis detected a significant, *positive* relationship. With respect to bone tissue, the medullary cavity is "empty space," and is thus inversely related to long bone diaphyseal strength. However, resistance to bending and torsional loads is enhanced by distributing bone further from the cross-sectional neutral axis of bending or the centroid, respectively. Thus, in two individuals with equal cross-sectional cortical areas, the one with the larger medullary area will have greater resistance to these loads. Thus depending on the context, medullary area can be either negatively or positively related to bone strength. It is the latter relationship that was detected in the factor analysis. It has also been argued, based on ontogenetic evidence, that the long bone medullary stenosis seen in most premodern human specimens is a function of elevated levels of activ-

ity during adulthood, not high levels of circulating steroids during adolescence (Ruff et al., 1994). Gracilization models overall, whether based on endocrine shifts or evolving material culture, cannot be entirely dismissed with the data at hand. However, it is clear that these models are not sufficient to account for much of the upper body morphological differences between archaic and modern humans.

The neo-Darwinian, particularist approach to interpreting morphological evolution is generally supported by the low level of trait intercorrelation (at least in this instance; epigenetic developmental shifts may play a much greater role in explaining phenotypic contrasts in comparisons conducted at higher taxonomic levels). Continued use of single traits or trait complexes in functional and phylogenetic studies of late archaic and early modern humans appears to be warranted. However, the phylogenetic valences of all postcranial traits need to be individually evaluated. Robusticity, for example, is a multidimensional feature with some aspects (cortical bone, size of muscle scars) being highly plastic. Accordingly, robusticity should not be used as a simple trait or character state in taxonomic or phyletic analyses (e.g., Stringer, 1987, 1993; Stringer and Andrews, 1988). The shape of two upper limb muscle attachment sites (scapular axillary border and deltoid tuberosity morphology—the two most commonly used in phylogenetic and taxonomic arguments involving Neandertals), on the other hand, appear to be little influenced by variation in other features, and may be the more useful phylogenetic indicators. While it is clear that the form of muscle scars undergoes age- and activity-related changes (e.g., Hoyte and Enlow, 1966; Robb, 1994), it seems equally clear that there are genetic bases to muscle-marking morphology and that some attachment sites may provide defensible phylogenetic markers.

The overall pattern of the morphological data suggests that Neandertals shared a common upper body bauplan with anatomically modern humans, and that behavior-specific activity effects and anatomical site-specific genetic evolution accounts for the wealth of the morphological contrasts in the

upper body between these groups. Given the great plasticity of skeletal tissue, and that much of the genetic evolution may have been selection driven, the mosaic nature of upper body evolution across the Neandertal/modern human boundary in all likelihood reflects activity level and behavior pattern changes indicating substantial adaptive shifts at this time. Concomitant shifts in material culture, especially resource extractive technology, signal more than just technological progress (which then brings somatic gracilization). These shifts likely reflect technological responses to pressure to change subsistence practices, something we see paralleled in somatic evolution in the later Pleistocene.

SUMMARY

1. A model of morphological integration between body form and upper limb traits in Pleistocene/Holocene *Homo* fits the data better than a model of no integration.

2. However, integration generally accounts for less than one-half of the variance in upper limb traits, indicating that there is a high degree of tolerance for particulate evolution in the context of an integrated body plan.

3. The strongest relationships detected (and those that must be considered in functional and phyletic analyses) involve (1) upper limb joint shapes and body size, (2) humeral shaft shape and body size and chest shape, and (3) biomechanical efficiency and measures of skeletal robusticity and muscularity.

4. Particulate uses of traits and trait complexes (for adaptive and phylogenetic analyses) appear to be warranted, but further research into the nature of postcranial morphological integration would be profitable.

ACKNOWLEDGMENTS

I thank Erik Trinkaus, Chris Ruff, Jeffrey Long, Robert Franciscus, Bettina Behrens, Robert Tompkins, Matt Cartmill, and two reviewers for helpful comments on this manuscript.

For access to fossil and comparative skeletal material, I thank R. Potts, B. Bronson,

D. Pilbeam, S. Rhine, B. Vandermeersch, M. Soubeyran, J.J. Cleyet-Merle, E. Ladier, H. de Lumley, A. Langaney, M.-H. Marino, R. Orban, J. Cordy, L. Seidl and J. Jelínek, J. Svoboda, J. Szilvassy, G. Grupe, A. Czarnecki, H. Joachim, J. Altuna, V. Formicola, F. Fedele, M. Guerri, F. Mallegni, G. Spadea, L. Tagliaferro and A.M. Pastorino, O. Giugliola, G. Rossi, G. Caldo, S. Simone, P. Wick, C. Simon, J. Radovčić, M. Paunović and the late M. Malez, C.B. Stringer, W.J. Kennedy, J. Zias and T. Arnon, and B. Arensburg and Y. Rak.

This research was supported by the L.S.B. Leakey Foundation, the National Science Foundation (BNS-9122068), and the University of New Mexico.

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APPENDIX: DEFINITION OF MEASUREMENTS

Overall body size was represented by the geometric mean (GEOMEAN) of three variables:

1. Humeral articular length: the distance from the proximal surface of the humeral head to the distalmost point on the lateral trochlear margin.

2. Radial articular length: Martin #2 (Martin, 1928).

3. Clavicular maximum length: Martin #1 (Martin, 1928).

Chest shape was represented by two variables:

1. Second rib chord (R2C): McCown and Keith (1939, Fig. 75).

2. Bi-iliac breadth (BIB): Martin #2 (Martin, 1928).

Robusticity was represented by four variables:

1. Radial tuberosity area (RTA): derived from the length and breadth of the bicipital tuberosity (Trinkaus, 1983b) using the formula for the area of an ellipse ($RTA = \pi * [0.5]length * [0.5]breadth$).

2. Humeral distal articular area (HDAA): calculated by modeling the articular surface as a partial cylinder and using the equation $HDAA = Diam * Ht * \cos^{-1}(1 - 2 * [depth / diam])$, where Ht = distal articular breadth (Martin #12a; Martin, 1928), $diam$ = the average of three AP diameters taken on the medial margin, center, and lateral margin of the trochlea, and $depth$ = capitular superoinferior diameter (maximum SI diameter of the capitular articular surface).

3. Humeral mid-distal polar moment of area (35%J): taken at 35% of humeral articular length measured from the distal end and determined from reconstructed cross sections (using dental putty external contour molds and multiple-plane radiography) input to SLICE (Nagurka and Hayes, 1980; Eschman, 1990) following the methods detailed in Churchill (1994a).

4. Humeral midshaft medullary area (50%MA): from reconstructed cross sections taken at 50% of humeral articular length.

Upper limb muscle morphology was represented by one variable (ultimately dropped from the analysis):

1. Relative deltoid tuberosity width (DEL-

TWID): taken as the residual of deltoid tuberosity width (Endo, 1971) on circumference (diaphyseal circumference taken at 5/12ths maximum humeral length).

Upper limb joint shapes were represented by two variables:

1. Scapular glenoid fossa shape (GLENOID): taken as the residual of glenoid articular breadth on length (Trinkaus, 1983b).

2. Ulnar trochlear notch orientation (TROCH): taken as the residual of olecranon height on coronoid height (McHenry et al., 1976, measurements 9 and 8).

Humeral diaphyseal shape was represented by two variables:

1. Humeral torsion angle (TORSION): Martin #18 (Martin, 1928).

2. Humeral midshaft cross-sectional theta (50% Θ): from reconstructed cross sections taken at 50% of humeral articular length.

Upper limb biomechanical efficiency was represented by two variables:

1. Deltoid efficiency (DELTOID): taken as the residual of deltoid tuberosity position (the distance in a coronal plane from the proximal surface of the humeral head to the point of convergence of the medial and lateral crests of the tuberosity) regressed on humeral articular length.

2. Biceps efficiency (BICEPS): taken as the residual of radial head-neck length (Martin #1a; Martin, 1928) on radial articular length.